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NEW AND INTERESTING *GOMPHONEMA* (BACILLARIOPHYCEAE) SPECIES FROM EAST AFRICA

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ABSTRACT: The taxonomy and ultrastructure of five *Gomphonema* Ehrenb. species from East Africa, including two described as new, are presented. Ultrastructure of East African species is compared with congeners and shown to differ in several aspects. *Gomphonema africanum* West, *G. aequatoriale* Hust., *G. kilhamii* sp. nov., and *G. paddockii* sp. nov. are endemic to the region and appear to be closely related by virtue of the unusual structure of their stigmata and lack of puncta occlusions. These species of *Gomphonema* may also be closely allied to *Gomphocymbella beccari* (Grun.) Forti, which has a similar, elongate stigma. *Gomphonema clevei* Fricke, which also appears to be endemic to East Africa, resembles *Reimeria sinuata* (Greg.) Kociolek & Stoermer with regard to stigma morphology. The systematic position of this putative group is unclear.

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INTRODUCTION

A large body of information on diatoms from East Africa has accumulated over the last century, including the works of Fricke (1902), Müller (1905), West (1907), Hustedt (1949), Cholnoky (1954), Kufferath (1956), Monteira (1963), and Gasse (1986). These important floristic works, and others (see Ross 1983; Gasse 1986 for extensive bibliographies) indicate *Gomphonema* Ehrenb. species are an important component of the region's diatom flora. Ross (1983) has noted *Gomphonema* species of the region are unique and has listed five species he considers endemics.

Despite the attention East African *Gomphonema* species have received, questions remain regarding circumscription of taxa. Reports on the morphology and distribution of *G. clevei* Fricke, for example, vary greatly (compare Fricke 1902 with Krammer and Lange-Bertalot 1986). Valve ultrastructure of most East African *Gomphonema* species is unknown; the only published observations are those of Gasse (1980) for a diatom identified as *G. africanum* West. Additionally, core material we have inspected from Lake Tanganyika contains specimens that appear to be new to science.

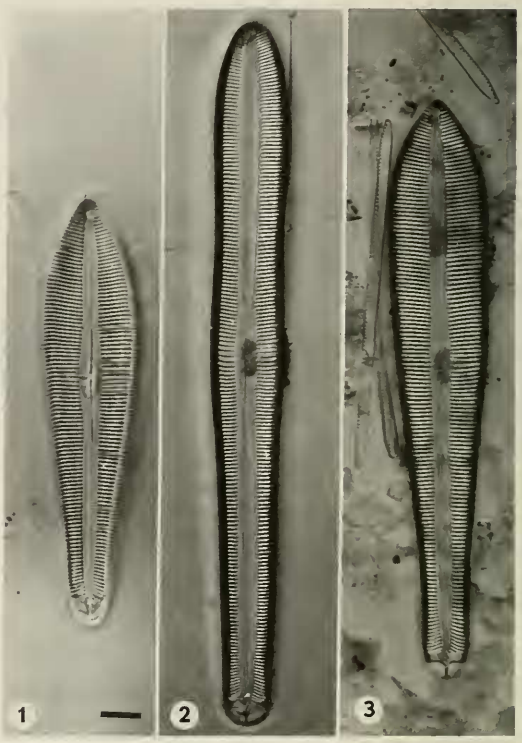
In this report we consider the taxonomy and

ultrastructure of five *Gomphonema* species from East Africa.

Materials and Methods

Observations were made on material from several sources. Cleaned material from cores taken from Lake Tanganyika was supplied to us by John Kingston (Queen's University). The original source of this material was Tom Johnson (Duke University). Samples from Lake Rudolf were taken by Robert Ross (The Natural History Museum, London), and material utilized in this study includes BM 1367, 1368, 1370, 1371, 1396, 1397, and 1398. This material, as well as the holotype slide for *G. africanum* from Lake Tanganyika, was kindly provided by David Williams of The Natural History Museum, London.

Material from these sources was boiled in nitric acid and alternately rinsed and settled in distilled water to remove oxidation by-products. Cleaned material was air-dried onto cover glasses and mounted onto microscope slides with Hyrax®. Light microscopic observations were made with Reichart Polyvar, Olympus OH-2, and Leitz Ortholux microscopes. For scanning electron microscopy (SEM), cover glasses containing air-dried material were mounted onto aluminum stubs and coated with approximately 20 nm of gold-palladium. Material was viewed on JEOL T-100 and Hitachi H-520 SEMs.



Figures 1–3. *Gomphonema africanum*, "clavate" type. Figure 1. Specimen from holotype slide, BM 78079, "Tanganyika 26-viii-'04, Cunnington 79." Figures 2, 3. Specimens from Lake Tanganyika, core, station 10, 100 cm. Scale bar = 10 μm.

Results

Gomphonema Ehrenberg 1832

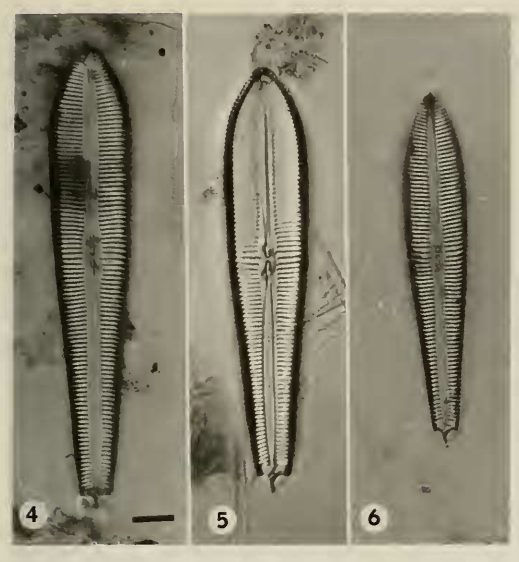
Gomphonema africanum West

(Figs. 1–21, 26)

Valves 70–230 μm long, 14–25 μm wide, and highly variable in outline. A number of distinct morphologies can be identified. One group, which includes specimens from the holotype slide (BM 78079), is strongly clavate, broadest near the headpole, and has "turris"-like/apiculate headpoles (Figs. 1–6). A second group (Figs. 7–9) is lanceolate-clavate and broadest at the center of the valve, while a third group is linear-lanceolate (Figs. 10–13). A prominent apical pore field (APF) positioned at footpole and one large spine visible at headpole (Fig. 11). Raphe lateral and straight. One to several stigmata have external openings near puncta, making them somewhat difficult to observe. Axial area narrow, becoming slightly wider around central area. Striae distinctly punctate and uniseriate. Striae radiate along most of length of valve, strongly radiate at footpole. Striae 8–12/10 μm and consistently finer at footpole. Small septum and pseudoseptum present at each pole.

In the SEM, external stigmal openings oblong relative to rounded puncta (Figs. 14, 15). Puncta unoccluded, but this may be caused by preservation problems on the subfossil specimens, which show other signs of valve degredation/dissolution (Fig. 16). External proximal raphe ends terminate close to one another (Fig. 15). Internally, central nodule bears recurved proximal raphe ends (Figs. 17, 18). Central nodule eccentric to raphe slit and stigmata project obliquely from near puncta onto it (Figs. 20, 21, 26). Pseudosepta visible at poles (Figs. 17, 19), and marginal lamina runs length of valve (Figs. 18, 26).

Comments.—These observations on general



FIGURES 4–6. *Gomphonema africanum,* "clavate" type, specimens from Lake Tanganyika, core, station 10, 100 cm. Scale bar = 10 μm.

valve morphology agree well with the original description of West (1907) and Hustedt's (1949) detailed treatment. The size range reported here is wider than previously recognized. Formal taxonomic recognition of the different morphologies described here awaits additional observations on shape variability, particularly of larger specimens.

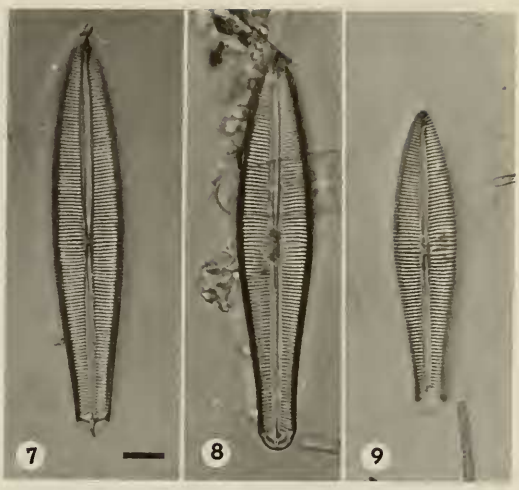
Foged's (1966) illustrations of this species from Ghana are more reminiscent of *G. gracilis* var. *turris* Hust. than *G. africanum.*

Gomphonema kilhamii, Kociolek & Stoermer, sp. nov.
(Figs. 22–25, 27–31)

DESCRIPTION.—Valves trullate in outline, 70–180 μm long, 12–21 μm broad, headpole acute, footpole rounded and broader than headpole. Striae parallel-radiate, distinctly punctate, 9–10/10 μm at mid-valve, 11–13/10 μm at poles. Axial area straight, narrow, and contains laterally expanded raphe. Isolated stigma conspicuous, located close to striae. Internal proximal raphe ends distinct. Small pseudoseptum present at each pole.

HOLOTYPE.—Light microscopic preparation 216039, CAS (Fig. 23).

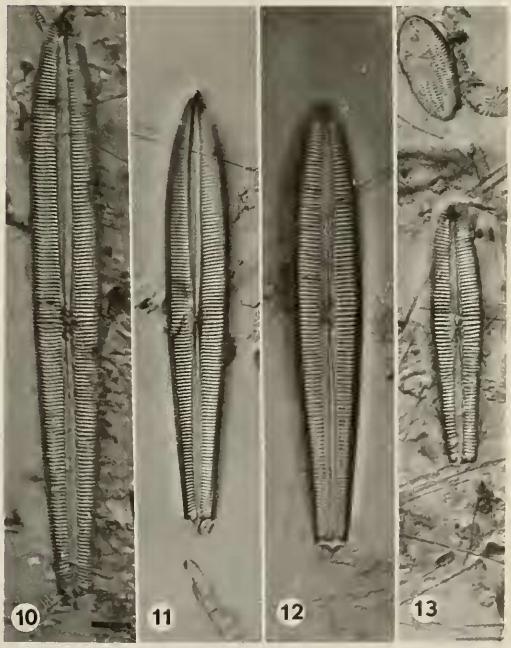
ISOTYPES.—Light microscopic preparations, ANSP and BM.



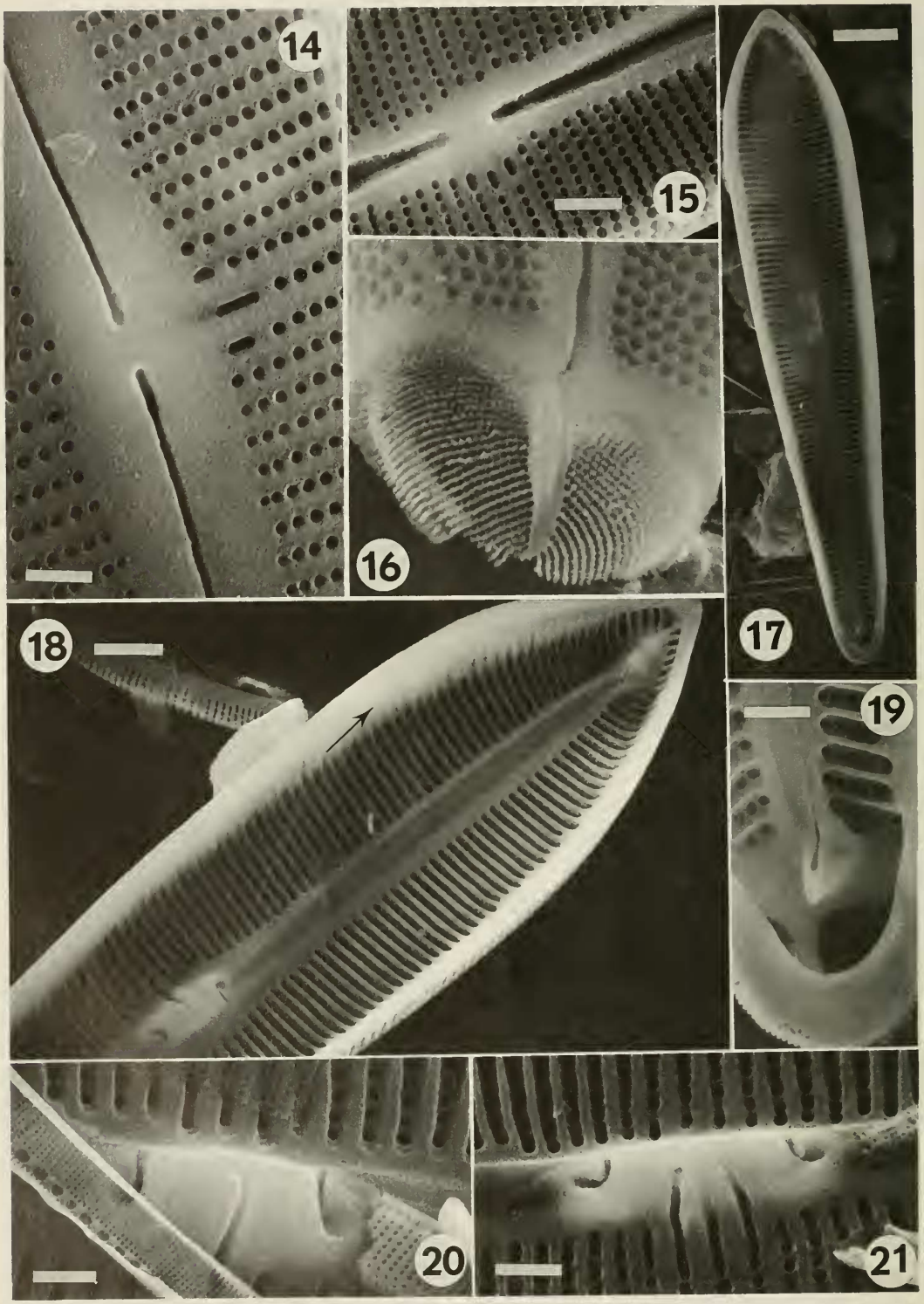
FIGURES 7–9. *Gomphonema africanum,* "lanceolate" type, specimens from Lake Tanganyika, core, station 10, 100 cm. Scale bar = 10 μm.

TYPE LOCALITY.—Lake Tanganyika, core, station 10, 100 cm.

In the SEM, puncta appear dash-like or narrowly tear-drop shaped (Figs. 27, 29, 30). External proximal raphe ends dilated and stigmal



FIGURES 10–13. *Gomphonema africanum,* "linear" type, specimens from Lake Tanganyika, core, station 10, 100 cm. Scale bar = 10 μm.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opening irregular and larger than puncta (Fig. 30). APF bisected by distal raphe end, producing different-sized lobes of APF. Porelli round and extend around raphe end along mantle (Fig. 29). At headpole, puncta slit-like and raphe curves onto mantle before reaching valve terminus (Fig. 27). Deflection of distal raphe end prior to valve terminus is unique among gomphonemoid diatoms studied thus far. Small projection occurs at headpole (Fig. 28). Internally, stigmal opening is an elongate slit, terminating on central nodule. Proximal raphe ends recurved. Pseudoseptum prominent and helictoglossa visible at headpole (Fig. 31).

COMMENTS.—This presumably extinct member of the Lake Tanganyika flora is distinguished by the angled, trullate shape of the valve. Although not abundant in the core material, specimens are easily recognized by the size and shape of the valves. Gasse's illustration identified as *G. africanum* (1980: pl. 50, Figs. 25, 26) resembles *G. kilhamii.* This species is dedicated to the late Peter Kilham, in honor of his work on African lakes.

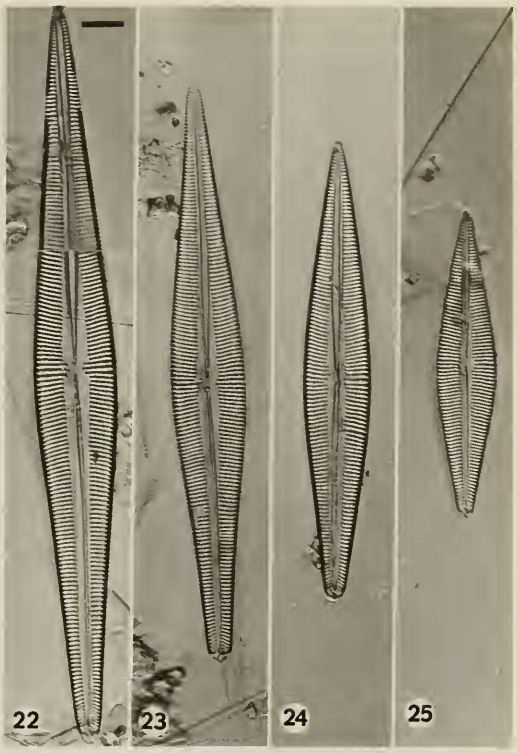
Gomphonema paddockii, Kociolek & Stoermer, sp. nov.
(Figs. 32, 33; 41, 42)

DESCRIPTION.—Valves broadly lanceolate-clavate, 94–103 μm long, 20–21 μm broad. Wide axial area, extending beneath striae, contains expanded, straight raphe. Striae radiate, strongly radiate at the footpole, 10/10 μm at mid-valve, 13–14/10 μm at poles. Stigma prominent, elongate, runs from central nodule towards striae.

HOLOTYPE.—Light microscopic preparation #216040, CAS.

ISOTYPES.—Light microscopic preparations, ANSP and BM.

TYPE LOCALITY.—Lake Tanganyika, core, station 10, 100 cm.



FIGURES 22–25. *Gomphonema kilhamii,* specimens from Lake Tanganyika, core, station 10, 100 cm. Scale bar = 10 μm.

In the SEM, recurved internal proximal raphe ends terminate on the edges of central nodule. Internal stigmal opening elongate and ends on central nodule (Figs. 41, 42).

COMMENTS.—This taxon is, like *G. kilhamii,* presumed extinct, since it is conspicuous but not previously reported in the many studies of Recent diatoms from Lake Tanganyika. This species is named in honor of T.B.B. Paddock, former Curator of Diatoms at the British Museum, for his excellent work on diatom taxonomy, ultrastructure, and systematics.

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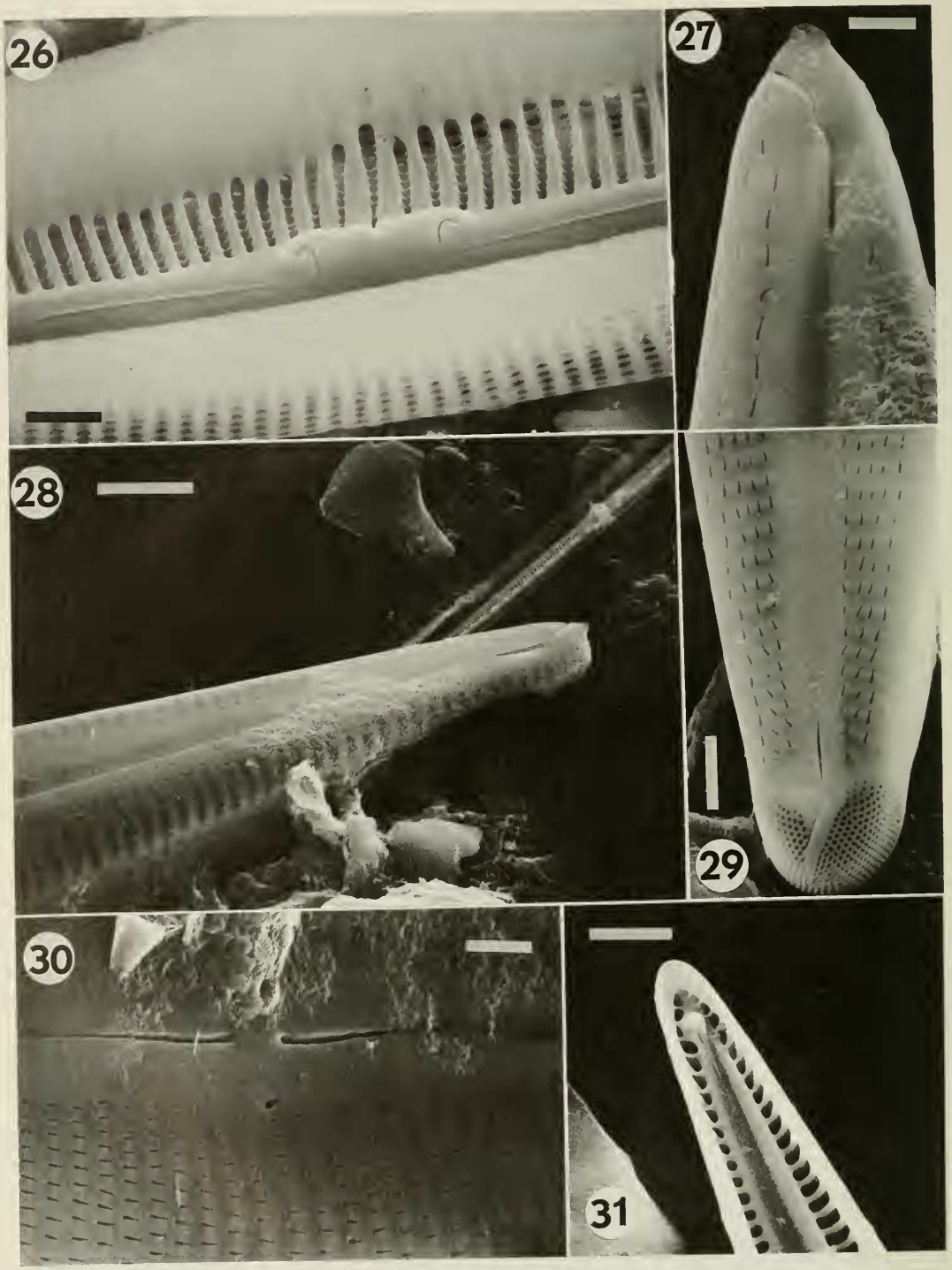
FIGURES 14–21. *Gomphonema africanum,* SEM, specimens from Lake Tanganyika, core, station 10, 100 cm. FIGURES 14, 15. External view of linear central area with elongated stigmal openings and round, unoccluded puncta. Scale bars = 2 μm and 2.8 μm, respectively. FIGURE 16. External view of footpole showing raphe bisecting apical pore field. Scale bar = 2.8 μm. FIGURE 17. Internal view of valve showing central nodule and poles with pseudosepta. Scale bar = 10 μm. FIGURE 18. Internal view of central nodule to headpole showing marginal lamina (arrow) and large helictoglossa. Pseudoseptum is visible near headpole. Scale bar = 5 μm. FIGURE 19. Internal view of footpole showing pseudoseptum and large helictoglossa. Scale bar = 2 μm. FIGURES 20, 21. Internal views of central nodule with recurved proximal raphe ends and elongate internal stigmal openings. Scale bars = 2 μm.



FIGURES 26–31. *Gomphonema* spp., SEM, specimens from Lake Tanganyika, core, station 10, 100 cm. FIGURE 26. *G. africanum,* internal view showing central nodule with recurved proximal raphe ends. Marginal lamina is visible. Scale bar = 3.5 μm. FIGURE 27. *G. kilhamii,* external view of headpole showing raphe curving onto mantle before terminus of valve. Scale bar = 1 μm. FIGURE 28. External view of headpole showing slit-like puncta and small protrusion at valve end. Scale bar = 3.5

Gomphonema aequatoriale Hustedt
(Figs. 34–40, 43–47)

Valves lanceolate-clavate 25–60 μm long, 8–10 μm broad, with headpoles squared-off and footpoles rounded. Striae punctate, parallel at headpole, becoming radiate towards central nodule. Striae radiate near footpole. Striae 8–10/10 μm near mid-valve, 10–13/10 μm at poles. External opening of single stigma positioned close to end of a median stria. Raphe lateral, slightly undulate. Prominent septa and pseudosepta present at poles.

In the SEM, puncta oblong, nearly circular or tear-drop shaped and usually uniseriate, although they may occur in rows of two. Occlusions lacking in puncta. External proximal raphe ends dilated and stigmal opening round (Figs. 43, 44). At headpole distal raphe end curves and terminates on mantle (Fig. 44). APF bisected by distal raphe end. Two lobes of APF porelli of different sizes (Fig. 45). Porelli round, similar in shape to puncta but much smaller in size. Pseudosepta present at poles and helictoglossae offset from raphe slit internally (Fig. 46). Recurved internal proximal raphe ends and an elongate stigmal opening present on central nodule (Figs. 46, 47).

Comments.—Hustedt (1949) described *G. aequatoriale* as being 50–100 μm long and 12–16 μm wide. Hustedt's measurements are almost exactly twice the values recorded for the populations from Lake Rudolf examined in this study. Simonsen's (1987: pl. 527, Figs. 16–20) illustrations of Hustedt's specimens range from 30–57.5 μm in length. Hustedt apparently erred in his illustrations and description of this species. Otherwise, populations described here are in accordance with Hustedt's (1949) observations.

Gomphonema clevei Fricke
(Figs. 48–59)

Valves lanceolate-clavate with broadly rounded or protracted headpole and rounded footpole, 15–39 μm long, 4–8 μm broad. Radiate striae 12–14/10 μm. Raphe lateral and undulate. Axial area narrow at poles, becoming broader towards center of valve. Single stigma present.

In the SEM, puncta have external flaps and puncta openings appear slit-like or c-shaped (Figs. 55–57). External proximal raphe ends dilated and stigmal opening round, positioned near proximal raphe ends (Fig. 55). Distal raphe ends deflected onto valve mantle (Figs. 55, 57). Porelli of APF round, unoccluded, and physically separated from puncta by unornamented area. In girdle view, each valve has two open, punctate girdle bands (Fig. 56). One band closed at headpole, other closed at footpole. Each cingulum has small septum. Pseudosepta and helictoglossae present at poles (Fig. 58). Raised central nodule bears recurved proximal raphe ends and round stigmal opening (Fig. 59).

Comments.—The taxonomy of *G. clevei* is poorly understood and this appears to have led to confusion regarding its distribution. Krammer and Lange-Bertalot (1986) suggest that *G. clevei* is cosmopolitan. Fricke (1902) illustrated a small group of East African specimens, 14.5–27 μm long and 4.5–6.5 μm broad, with 9–13 striae per 10 μm, and recent figures by Gasse (1986) are similar to Fricke's original illustrations. Müller (1905) described *G. brachyneura,* a linear-lanceolate species also from East Africa, as 16–34 μm long, 4–5 μm wide, and having 13–15 striae in 10 μm; and Cholnoky (1954) considered *G. clevei* and *G. brachyneura* conspecific. Hustedt's (1938) concept of *G. clevei* from Java, Bali, and Sumatra appears to be different from Fricke's (Krammer and Lange-Bertalot 1986), in that Hustedt's figures have a more linear valve outline and broader axial area (Hustedt 1938; see also Krammer and Lange-Bertalot 1986). Hustedt also described *G. clevei* var. *javanica* Hust., which differs markedly from the nominate variety in shape of the valve and striae pattern (Hustedt 1938; Simonsen 1987). Subsequent reports of *G. clevei* made from Europe (Foged 1977, 1979), America (Patrick *in* Patrick and Reimer 1975; Camburn et al. 1978) and Australia (Foged 1978) appear to follow Hustedt's concept of this species. A reconsideration of the material of Hus-

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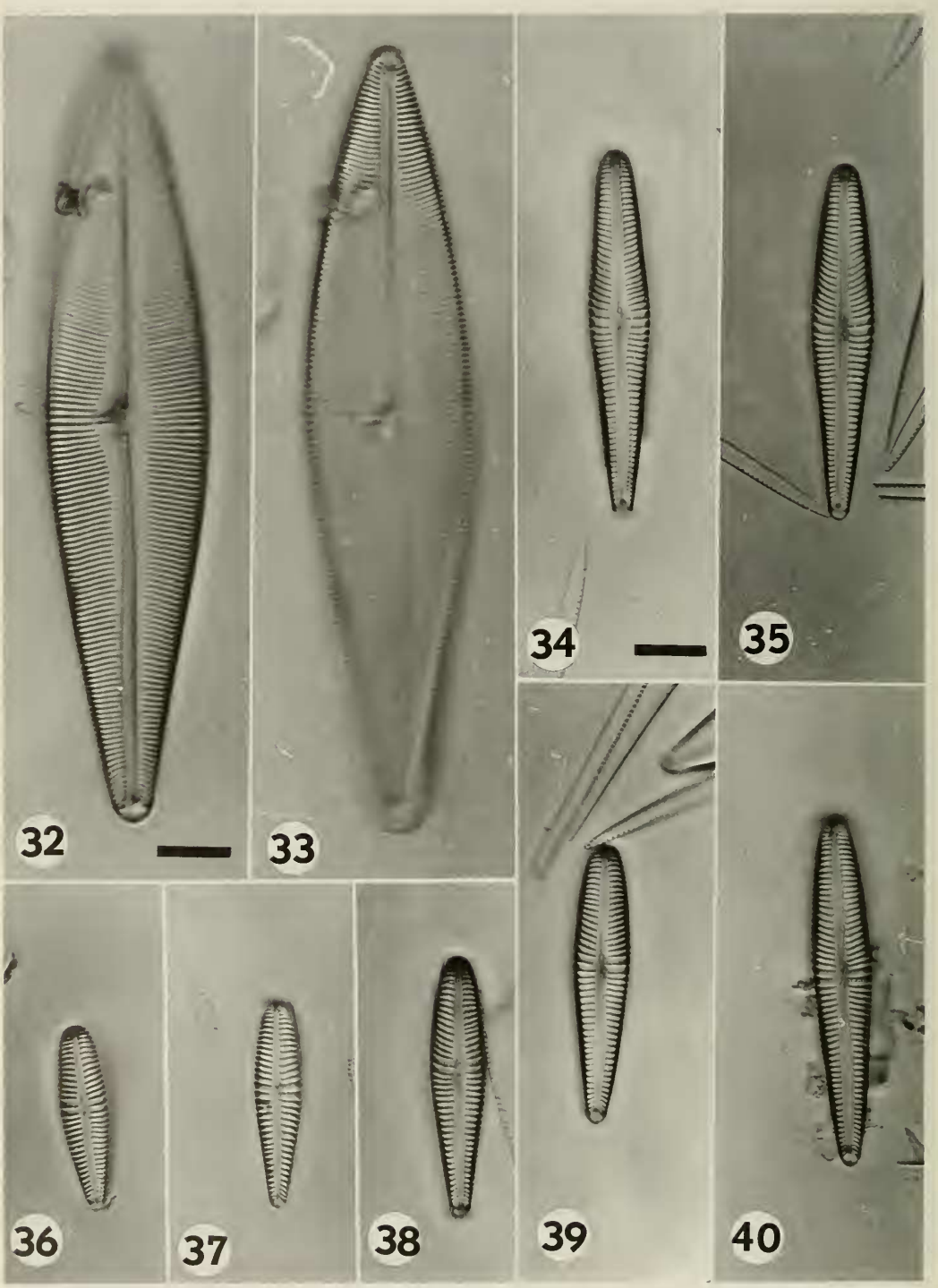
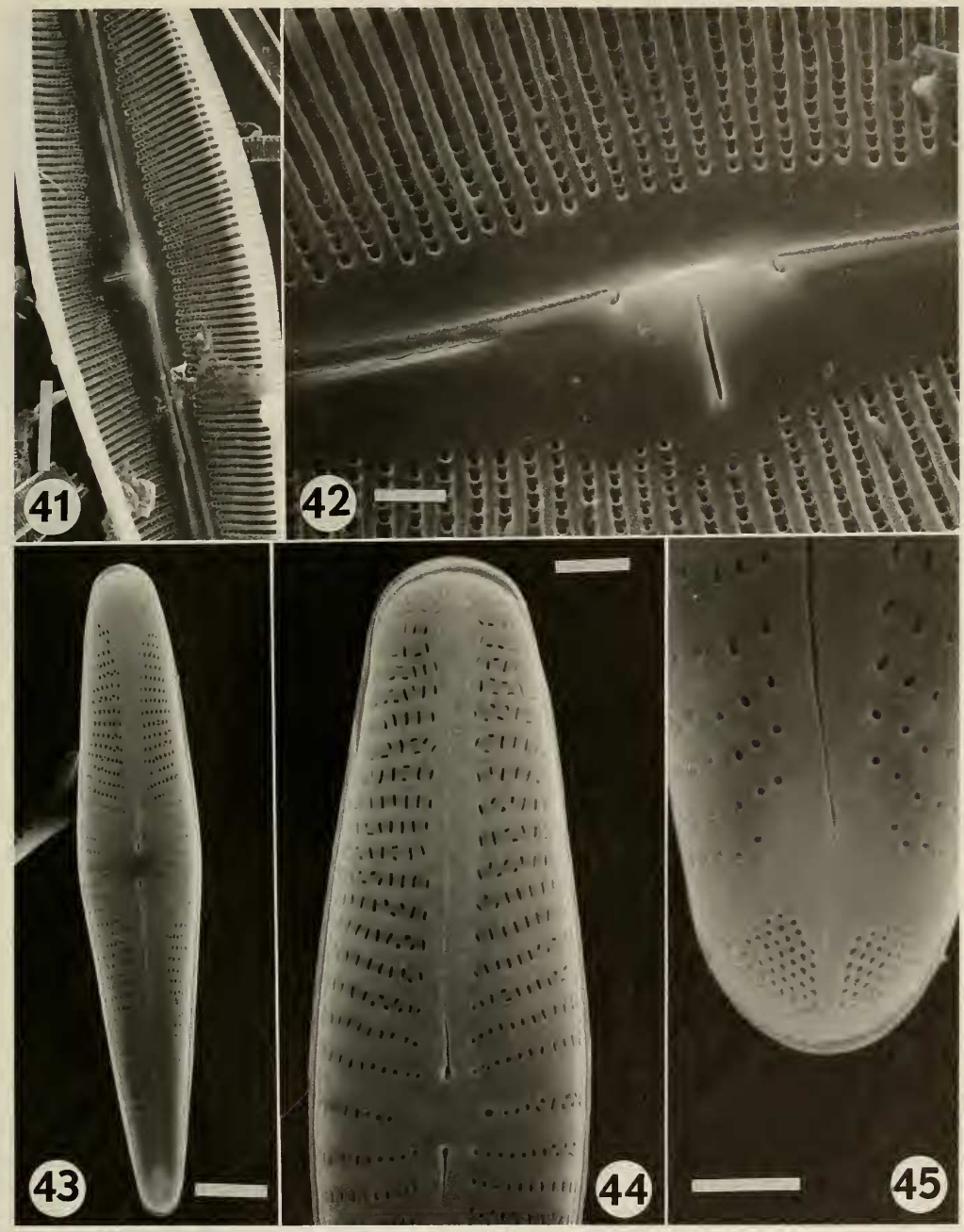
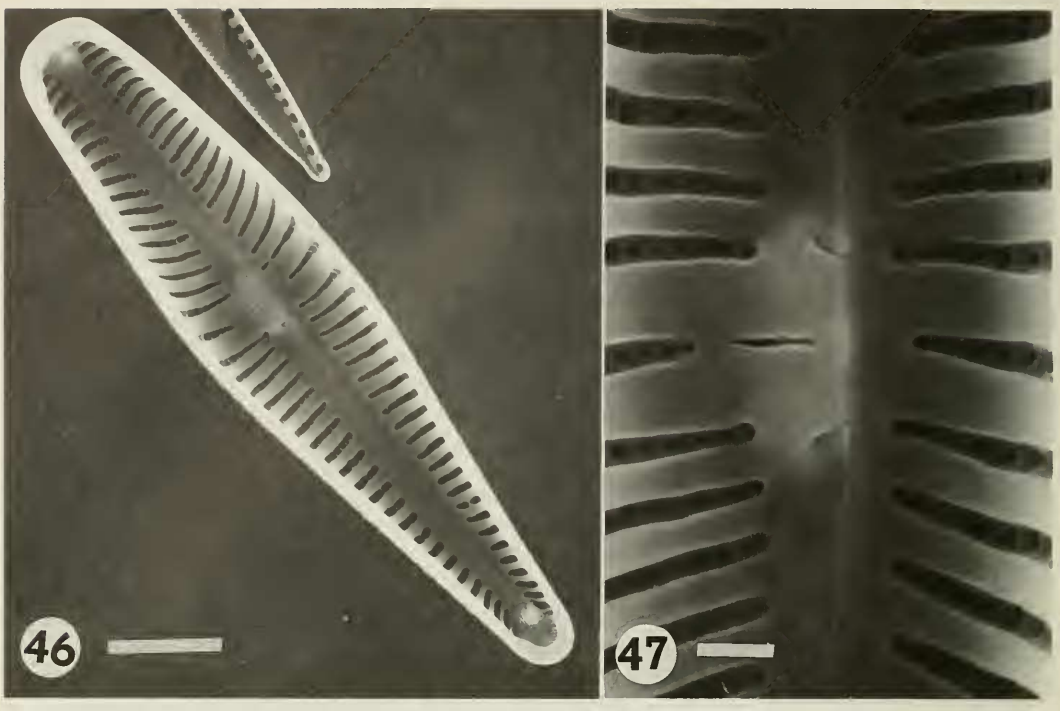
μm. Figure 29. External view of footpole showing bilobed apical pore field, with lobes being of different sizes. Porelli are round and extend around distal raphe end on valve mantle. Scale bar = 2 μm. Figure 30. External view of central area showing tear drop shaped puncta, rounded stigmal opening, and dilated proximal raphe ends. Scale bar = 2 μm. Figure 31. Internal view of headpole showing prominent pseudoseptum. Scale bar = 3.5 μm.



FIGURES 32–40. *Gomphonema* spp. FIGURES 32, 33. *G. paddockii,* specimen from Lake Tanganyika, core, station 10, 100 cm. FIGURES 34–40. *G. aequatoriale,* specimens from Lake Rudolf. Scale bar = 10 μm.



FIGURES 41–45. *Gomphonema* spp., SEM. FIGURES 41, 42. *G. paddockii,* specimens from Lake Tanganyika, core, station 10, 100 cm, internal views of central nodule showing recurved proximal raphe ends and elongate stigmal opening. Scale bars = 10 μm and 2 μm, respectively. FIGURES 43–45. *G. aequatoriale,* specimens from Lake Rudolf, external views. FIGURE 43. Valve view showing outline, narrow axial area and dilated proximal raphe ends. Scale bar = 5.5 μm. FIGURE 44. Central nodule to headpole, with slit-like striae, round stigmal opening, and distal raphe end extending onto valve mantle. Scale bar = 2 μm. FIGURE 45. Footpole with bilobed apical pore field. Porelli are round and smaller than puncta. Scale bar = 1.3 μm.



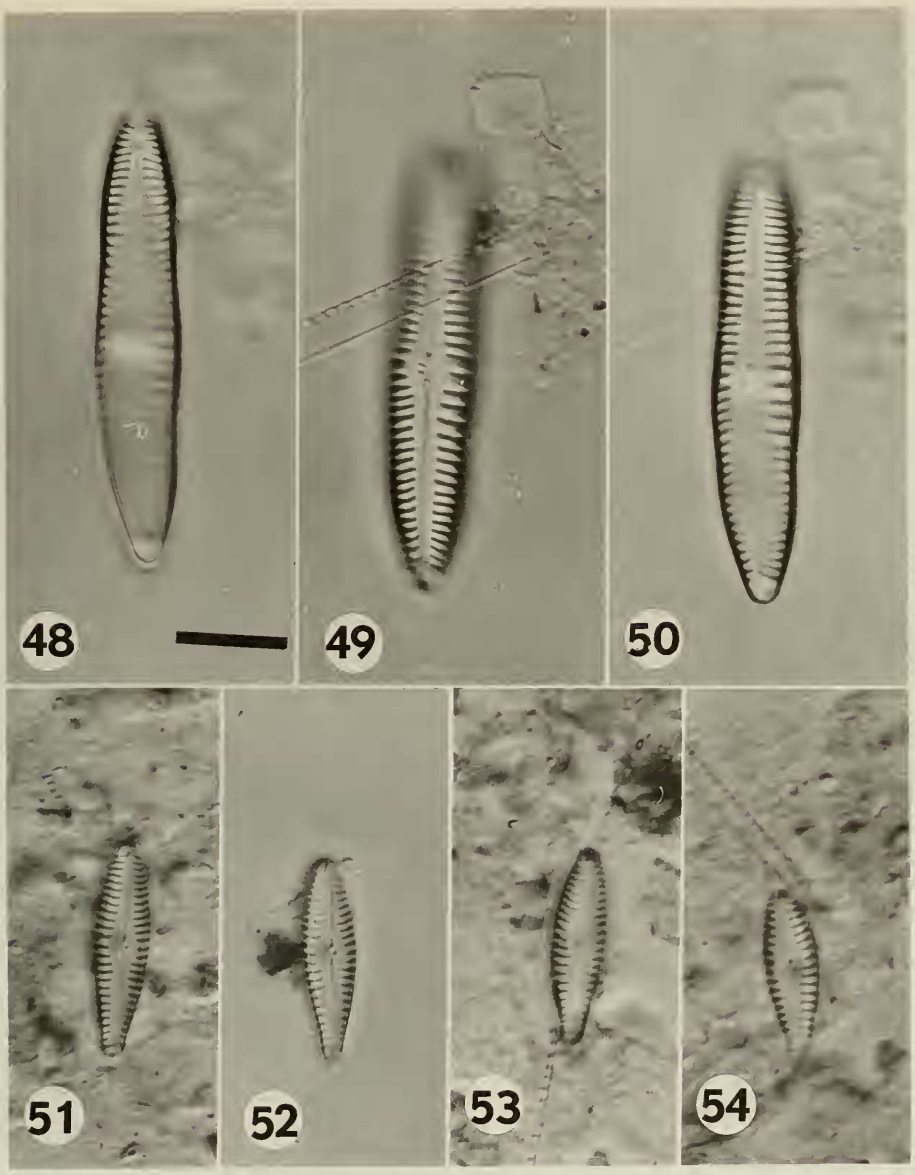
FIGURES 46–47. *Gomphonema aequatoriale,* SEM, specimens from Lake Rudolf, internal views. FIGURE 46. Valve view showing pseudosepta and helictoglossae at poles and internally raised central nodule. Scale bar = 5 μm. FIGURE 47. Central nodule with broadly recurved proximal raphe ends and elongate stigmal opening. Scale bar = 1 μm.

tedt, Foged, and others is necessary to determine if *G. clevei* is indeed cosmopolitan or just a complex of superficially similar taxa. Such a reconsideration may also determine if Fricke's species is limited to East Africa.

Krammer and Lange-Bertalot (1986: pl. 164, Figs. 17–19) suggest intermediate morphologies exist between *G. angustatum* Agardh (=*G. intricatum* Kützing, Kociolek and Stoermer in press c), *G. rhombicum* Fricke, and *G. clevei.* The specimens illustrated by Krammer and Lange-Bertalot do not appear to us to resemble one another except in outline of the valves. The individuals are small (all about 20 μm), although it has been well-documented that small specimens of different taxa tend to converge on similar shapes during size diminution (Geitler 1932). With reference to groups of *Surirella* Turpin species, Krammer and Lange-Bertalot (1987) have stated, "... if the smaller stages are examined ... the general uniformity in valve outline and valve surface hardly allows the two groups to be separated." Krammer and Lange-Bertalot's reference to the need to look at "entire populations" (1987) to make "correct identifications" of *Surirella* species is equally applicable to *Gomphonema* species.

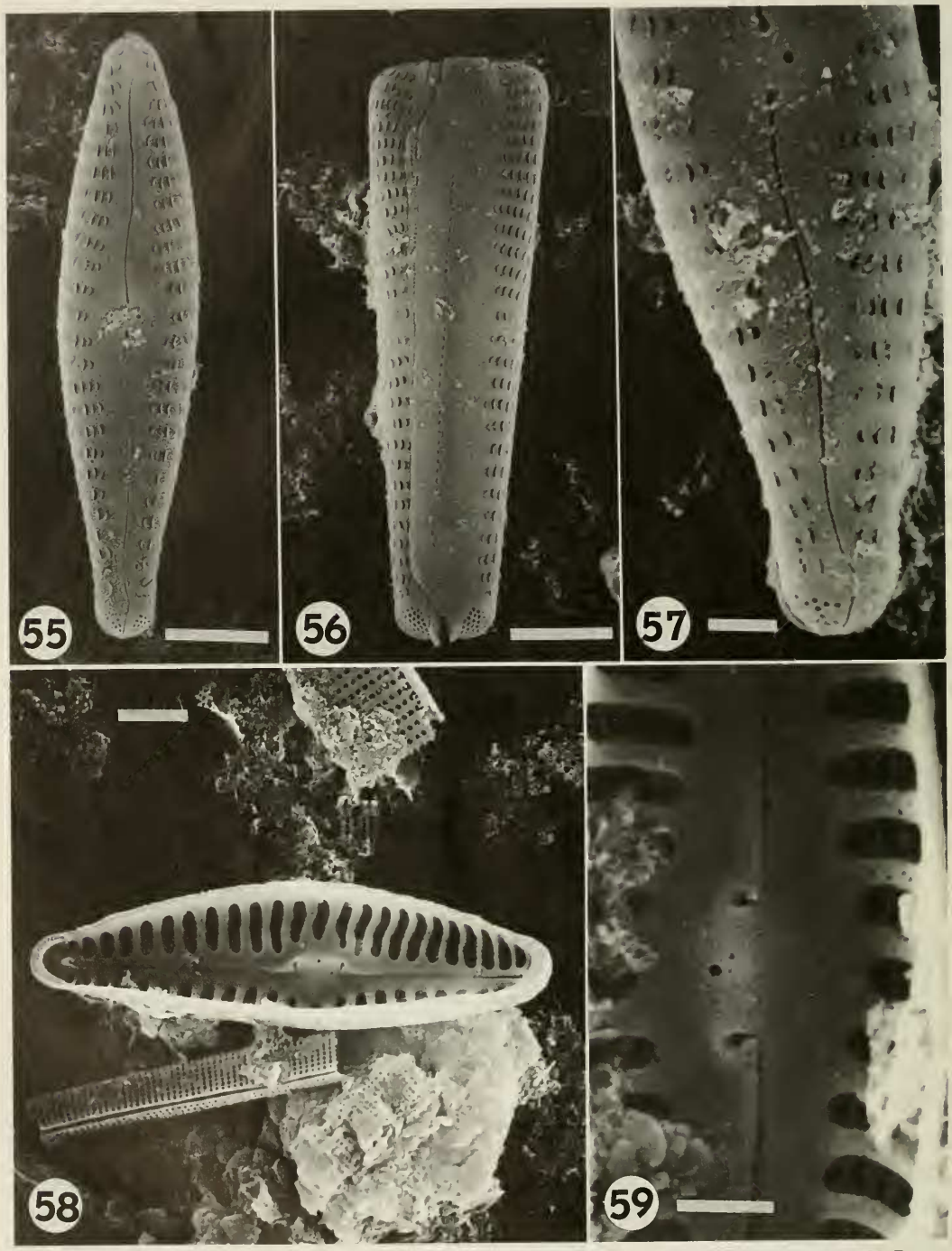
Discussion

Four of the five *Gomphonema* species considered here appear unique relative to other previously investigated members of the genus on the basis of valve morphology. *Gomphonema africanum, G. aequatoriale, G. kilhamii,* and *G. paddockii* all have elongated internal stigmal openings and lack siliceous occlusions in the puncta. Most "typical" *Gomphonema* species have short, slit-like internal stigmal openings that reside mainly on the central nodule (e.g., Dawson 1972, 1973) and have siliceous occlusions on the exterior or interior of the puncta (Kociolek and Stoermer 1990a, in press). These East African species are apparently endemic to the region and, considering their morphological similarities, may represent a distinct clade. These East African



FIGURES 48–54. *Gomphonema clevei*, specimens from Lake Tanganyika, core, station 1, 20 cm. FIGURES 48–50 are of an auxospore valve (?) at different levels of focus. Scale bar = 10 μm.

species may also represent the sister group to *Gomphocymbella beccari* (Grun.) Forti, an East African endemic which also has a similar stigma structure (Round et al. 1990; pers. obs.). The observation of a group of closely related *Gomphonema* species in East African Rift Valley lakes is similar to the report by Kociolek and Stoermer (1988b) of sister taxa of the *Gomphoneis quadripunctata* species complex from Lake Baikal. These reports of evolutionary lineages of gomphonemoid diatoms from specific geographic areas suggest that other regions with endemic species are worthy of examination (e.g., Indo–Malaysian Archipelago, Hustedt 1942), and this may ultimately lead to a new understanding of freshwater diatom biogeography.



FIGURES 55–59. *Gomphonema clevei*, SEM, specimens from Lake Tanganyika, core, station 1, 20 cm. FIGURE 55. External view of valve showing flap-like occlusions of puncta projecting away from valve surface. Raphe is undulate and stigmal opening is small and round. Scale bar = 3 μm. FIGURE 56. External view of girdle showing punctate, open girdle bands and round porelli of the apical pore fields. Scale bar = 3 μm. FIGURE 57. External view of central nodule to footpole showing round stigmal opening, occluded puncta, and undulate raphe with dilated proximal ends. Scale bar = 1 μm. FIGURE 58. Internal valve view showing internally raised central nodule and pseudosepta at the poles. Scale bar = 2 μm. FIGURE 59. Internal view of central nodule with recurved proximal raphe ends and round stigmal opening. Scale bar = 1 μm.

The other species considered here, *G. clevei,* also appears distinct from most other "typical" members of the genus. Although *G. clevei* has puncta occluded by flaps as well as other attributes in common with *Gomphonema* species (e.g., a single, bilobed APF and asymmetry about the transapical axis), it possesses a simple, round, internal stigmal opening. The structure of the internal stigmal opening of *G. clevei* resembles that of *Reimeria sinuata* (Greg.) Kociolek & Stoermer (Schoeman and Archibald 1978; Kociolek and Stoermer 1987) and *Cymbella diluviana* (Krasske) Florin (Kociolek and Stoermer 1990b). A number of authors have suggested a close relationship between *Reimeria* Kociolek & Stoermer and gomphonemoid diatoms (e.g., Krammer 1982; Round et al. 1990), while Kociolek and Stoermer (1988a) have suggested *Reimeria* is more closely related to cymbelloid diatoms. If the type of stigmal opening found in *G. clevei* and *Reimeria* is a derived condition, it may support the view of a close relationship between these two taxa. How this relationship is considered in the context of cymbelloid-gomphonemoid diatom phylogeny is, at present, unclear.

The five East African *Gomphonema* species treated here appear to be endemic to the region (pending taxonomic review of *G. clevei*), and this expands Ross's (1983) list of endemics for the East African flora. Additional studies appear warranted to determine if the level of endemism exhibited by Recent diatoms in East Africa mirrors the high levels found for other organisms. The apparent extinction of *G. kilhamii* and *G. paddockii* suggests that levels of endemic diatom species in East Africa may have been higher in the recent past. Other apparently endemic *Gomphonema* species are known from local diatomites (e.g., *G. swatmanii* Reinhold). Further studies are needed to document species and their distributions through time to determine if levels of endemism and diversity have changed in the region.

Acknowledgments

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